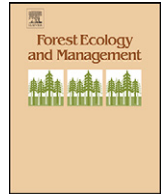


# **EXHIBIT K**



# Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: Evidence of a landscape configuration effect

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## ABSTRACT

Habitat alteration caused by forest harvesting seems to contribute to the decline of forest-dwelling caribou, an ecotype of woodland caribou (*Rangifer tarandus caribou*) inhabiting the boreal ecosystem. To serve as basework to the establishment of conservation measures for the species, we have studied the hierarchical habitat selection of forest-dwelling caribou in a boreal landscape of Québec strongly impacted by logging. Fifteen females were surveyed by GPS telemetry between April 2004 and March 2006. Home ranges showed a high proportion of 90–120 year-old forests, a low proportion of regenerating forests (20–40 years old) and a tendency to include a greater proportion of 6–20 year-old clearcuts in relation to their availability in the study area. At the home range scale, selection patterns differed between periods, possibly reflecting specific requirements linked to caribou life cycle. Caribou selected open lichen woodlands throughout the year while mature closed forests ( $\geq 50$  years) were selected uniquely during summer. The 6–20 year-old clearcuts were avoided during calving, in summer and during the rutting period but were selected during spring. Our results indicate that mature forest and open lichen woodlands are highly selected forest cover types by caribou at both spatial scales. Although clearcuts were generally avoided at the home range scale, such avoidance was not observed at the larger scale, the search for 90–120 year-old forests being hampered by a uniform distribution of clearcuts. An *a posteriori* landscape analysis highlighted the spatial association between 6–20 year-old clearcuts and 90–120 year-old forests, an association that can be explained by the current regulations used in Québec. Our results underline the importance of pursuing research concerning the impact of such an exploitation regime on the long-term maintenance of the forest caribou in the boreal landscape.

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## 1. Introduction

Forest harvesting is currently the main disturbance in most of the boreal forest. It has often been identified as being responsible for the decrease in abundance of many species at the boreal forest scale (e.g., Potvin et al., 1999; Lindenmayer and Franklin, 2002). The situation of the forest-dwelling caribou (*Rangifer tarandus caribou*), an emblematic species of the boreal forest, has become precarious. During the 19th and 20th centuries, important changes in the distribution and abundance of forest-dwelling caribou have been observed across Canada (Courtois et al., 2003; Schaefer, 2003). These changes have led the ecotype to be designated as a threatened species in Canada since 2002 (COSEWIC, 2006) and a vulnerable species in Québec since 2005 (MRNF, 2007).

Numerous studies refer to anthropogenic habitat modifications to explain decreases in numbers and even the extinction of many caribou herds across Canada (e.g., Smith et al., 2000; Vors et al., 2007; Wittmer et al., 2007). Not only have logging practices lead to important caribou habitat losses, they have also indirectly influenced population levels by increasing predation risk, the main natural limiting factor for forest-dwelling caribou populations (Rettie and Messier, 1998; James et al., 2004; McLoughlin et al., 2005). Forest logging leads to the overrepresentation of early successional stands, therefore providing greater quality habitat for moose (*Alces alces*) (Courtois et al., 1998). Such a forest structure composition change can favor the recruitment of alternative prey, thereby also increasing wolf population density (*Canis lupus*), the caribou's main predator (Rettie and Messier, 1998; James et al., 2004). Logging practices can also be beneficial for the black bear (*Ursus americanus*), since cutblocks are favorable to the growth of wild berries, a predominant item in its summer diet in the boreal forest (Brodeur, 2007; Mosnier et al., 2008).

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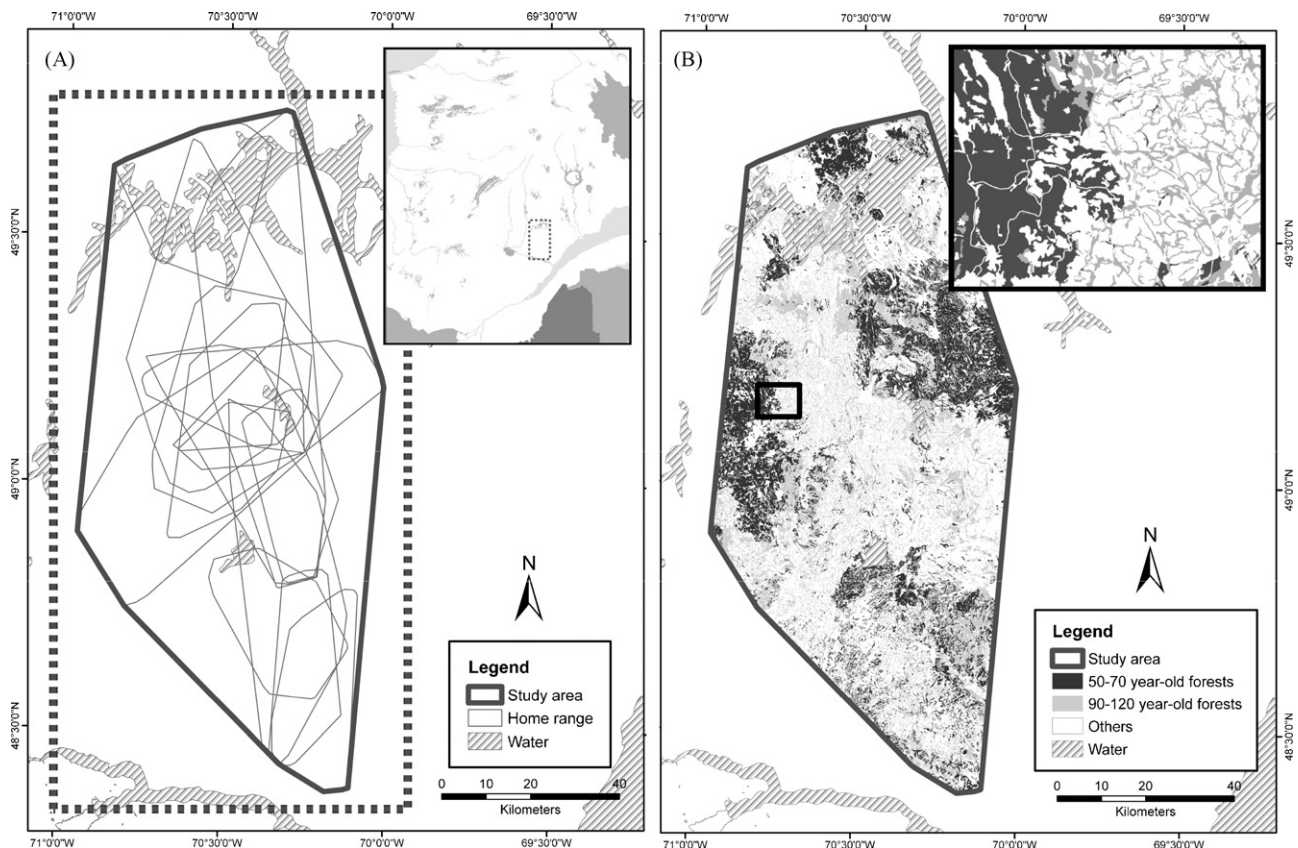
Furthermore, it has been shown that the black bear has been the leading cause of death in newborn caribou in the Charlevoix population of Québec (Lambert et al., 2006).

Habitat selection is considered a hierarchical process (Johnson, 1980; Orians and Wittenberger, 1991) where selection patterns should be modulated by factors that may reduce an individual's fitness and for which the importance varies according to the considered spatial scale (Rettie and Messier, 2000). Therefore, a factor showing strong potential for limiting fitness could dictate selection patterns at a larger scale. Once its impacts are attenuated, fine scale selection behavior will aim at minimizing the effects of limiting factors of lesser importance. Thus, selection scale will reflect a hierarchy in the various limiting factors, therefore supporting the necessity to perform selection studies at numerous spatial scales (Rettie and Messier, 2000; Dussault et al., 2005). Many studies on caribou habitat selection in western Canada with habitat selection as the main subject have defined cover types searched for by forest caribou in exploited boreal forest (e.g., Rettie and Messier, 2000; McLoughlin et al., 2005; Wittmer et al., 2007). Considering that harvest methods, the rate of harvest and harvest intensity differ between western and eastern Canada (Bourgeois et al., 2007), the main objective of our study was to investigate hierarchical habitat selection by forest-dwelling caribou in a boreal forest landscape disturbed by logging activities in eastern Canada where the rate of harvest and harvest intensity are higher than in western Canada. In addition, the most common harvest practices in western Canada are large cutblocks while in eastern Canada smaller cutblocks are generally interspersed within a mosaic of mature forests. These differences in harvest practices may impact habitat use of caribou, for example by forcing caribou in eastern

Canada to cross cutblocks between patches of mature forests while caribou in western Canada would avoid larger cutblocks altogether. Earlier studies have shown the importance of mature conifer forest in the selection of habitat by caribou (e.g., Terry et al., 2000; Ferguson and Elkie, 2004; Wittmer et al., 2007). In addition, a number of studies suggest a negative impact of disturbed landscapes on the population dynamics and habitat use of forest-dwelling caribou (Schaefer, 2003; Courtois et al., 2007; Schaefer and Mahoney, 2007). Even though cutblocks are interspersed within large patches of mature forests in eastern Canada, we hypothesized based on previous studies that mature forests should be selected by caribou while cutblocks should be avoided compared to their relative availability at both spatial scales (i.e., study area and home range).

## 2. Study area

This study was done in the Saguenay Lac St-Jean region, Québec, Canada, between 48°23' and 49°46' N and 70°01' and 70°57' W (Fig. 1A). The study area covers 7,535 km<sup>2</sup> and overlaps two bioclimatic zones known as the white birch–balsam fir forest to the south and black spruce forest to the north. Representative tree species are the black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and to a lesser extent, white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*). Mature forest understory consisted mainly of moss and ericaceous species. The area is subjected to a mean annual precipitation varying from 900 to 1300 mm and a mean annual temperature of 0.0 °C (Robitaille and Saucier, 1998). Between 2003 and 2006, a mean maximal snow depth of 1.45 m was recorded in



**Fig. 1.** (A) Location of the study area and home ranges of caribou ( $n = 15$ ) tracked between April 2004 and March 2006, Saguenay, Québec. (B) Distribution of two types of mature forest (50–70 and 90–120 year-old forests) within the study area. The box allows for visualizing the mature forest configuration, represented as large blocks for 50–70 year-old forests and residual strips for 90–120 year-old forests.

the area (University of Québec at Chicoutimi, unpublished data). The study area is mainly located on public lands and is subjected to commercial logging following provincial regulations. In 2004, nearly 25% of the territory had been harvested during the last 20 years, mainly using a cutting with protection of regeneration and soils (CPRS) harvest method. Approximately 40% of the forest territory under study was previously covered by coniferous dominant stands not affected by logging whereas those characterized by deciduous stands only represented 5% of the study area. The caribou population under study is in the transition zone between the southern limit of the forest-dwelling caribou distribution area and the northern limit of forest logging activities in the province.

### 3. Methods

#### 3.1. Telemetry survey

Between April 2004 and March 2006, we captured 25 adult females by net-gunning from a helicopter (Potvin and Breton, 1988) and fitted them with GPS (Global Positioning System) collar transmitters (Lotek® models 2200L and 3300L). During the first survey year, four females died, four had collar failures and we lost contact with two others. In total, 15 adult female caribou were tracked on an annual basis. Moreover, we only considered individuals with a minimum of one year of tracking in the data analysis. Of the 15, eight were tracked over the 2 years of the study while the seven others were only followed during one year (i.e., five between April 2004 and March 2005 and two between March 2005 and March 2006). The collars allowed the recording of 12 (the 2200L) and 24 (the 3300L) locations per day. We kept all 2D and 3D locations for which the precision's dilution value (PDOP) was inferior to 10 to obtain a tracking accuracy better than 20 m (Dussault et al., 2001). The mean number of locations per individual was  $4594 \pm 2083$  (S.D.).

#### 3.2. Habitat categories

The forest caribou habitat selection evaluation was done using digitized ecoforest maps provided by the Ministère des Ressources naturelles et de la Faune du Québec. We grouped forest polygons into 10 habitat categories representative of the area under study while considering the precision of the ecoforest map (Table 1).

Seven forest habitat categories were created according to forest stand age and considering known forest caribou habitat requirements. Two types of forest cuts were first used: '0–5 year-old clearcuts' and '6–20 year-old clearcuts', to better capture short and mid term effects of mature forest cover loss. Following age classification of ecoforest maps, 'Regenerating forests' refers to forests of ~30 years of age (ranging from 20 to 40 years) issued from a natural or an anthropogenic disturbance. The mature forest was divided into two categories according to ecoforest maps: '50–70 year-old forests' (i.e., ranging from 40 to 80 years old) and '90–120 year-old forests' (i.e., >80 years old). We used this subdivision of closed canopy forest to consider the age of commercial maturity which is set at 90 years for black spruce forest. Although lightly available at the scale of the study area, 'Open lichen woodlands' (i.e. black spruce stands of density inferior to 25% showing a lichen ground cover greater than 40%) and 'Peatlands' each formed a habitat category since they have been identified as preferred habitat for caribou (McLoughlin et al., 2005). Furthermore, because they are abundant in the study area, 'Water' (i.e., water ways and bodies) as well as 'Roads' also formed two distinct non-forested habitat categories. Finally, we grouped all other stand types (e.g. alder (*Alnus* spp.), recent burns) or non-forested habitats (e.g. sand pits, hydroelectric power lines) that were weakly represented in the study area into the category 'Others'.

We surveyed the seven habitat categories during summer 2005 in order to validate classifications for all pre-identified forest stand types and to refine the information given by the ecoforest maps in relation to stand undergrowth vegetation composition and structure. We conducted a systematic inventory of all lignous stems in a variable radius circular plot in order to calculate mean stem density as well as basal area in 15 plots in each of the seven habitat categories. Trees for which the diameter at breast height (DBH) was >9 cm were counted in 11.28-m radius circular plots (400 m<sup>2</sup>), while smaller trees (DBH 1–9 cm) were counted within 5.28-m radius circular plots (100 m<sup>2</sup>) and those <1 cm DBH were tallied within 2.82-m radius circular plots (25 m<sup>2</sup>). We evaluated the mean height of tree and shrub strata from 10 stems representative of each stratum within each site. The age of forest polygons indicated on the ecoforest maps were used as reference for each site. We estimated the relative abundance of herb and moss strata and of terrestrial lichens in proportion of ground cover (10% classes) in a 1-m quadrat centered in the initial circular plot as well as at a distance of 15 m from the plot center in each cardinal

**Table 1**  
Description of habitat categories used to evaluate habitat selection by forest caribou in harvested boreal forest. Means are shown for each variable, and different letters represent significant differences following a Tukey multiple comparison test.

| Category                | Description <sup>a</sup>   | Basal area of commercial stems (DBH ≥ 9 cm) (m <sup>2</sup> /ha ± S.D.) | Basal area of noncommercial stems (DBH < 9 cm) (m <sup>2</sup> /ha ± S.D.) | Canopy closure (% ± S.D.) | Terrestrial lichen cover (% ± S.D.) |
|-------------------------|--|---|--|---------------------------|-------------------------------------|
| 0–5 year-old clearcuts  | CPRS for which harvest date ≥2001  | 0.2 ± 0.3 <sup>A</sup>  | 4.1 ± 5.9 <sup>A</sup>   | 3 ± 4 <sup>A</sup>        | 0 ± 1 <sup>ABC</sup>                |
| 6–20 year-old clearcuts | Total clearcuts or CPRS harvested between 1986 and 2001                      | 1.1 ± 1.8 <sup>A</sup>  | 9.1 ± 7.4 <sup>AC</sup>  | 12 ± 16 <sup>A</sup>      | 4 ± 15 <sup>ABC</sup>               |
| Regenerating forests    | Forest stands with dominant tree strata ranging from 20 to 40 years old      | 11.4 ± 9.3 <sup>B</sup>   | 24.3 ± 11.9 <sup>B</sup>   | 51 ± 19 <sup>B</sup>      | 4 ± 11 <sup>AB</sup>                |
| 50–70 year-old forests  | Forest stands with dominant tree strata ranging from 40 to 80 years old      | 20.7 ± 9.0 <sup>C</sup>   | 13.4 ± 9.3 <sup>C</sup>  | 52 ± 16 <sup>B</sup>      | 6 ± 13 <sup>B</sup>                 |
| 90–120 year-old forests | Forest stands with dominant tree strata >80 years old                        | 19.8 ± 7.4 <sup>C</sup>   | 11.1 ± 5.1 <sup>CD</sup>   | 52 ± 16 <sup>B</sup>      | 2 ± 11 <sup>C</sup>                 |
| Peatlands               | Non-productive humid forest  | 1.7 ± 2.9 <sup>A</sup>  | 5.6 ± 5.9 <sup>A</sup>   | 5 ± 5 <sup>A</sup>        | 0 ± 1 <sup>ABC</sup>                |
| Open lichen woodlands   | Non-productive dry forest  | 6.6 ± 3.5 <sup>B</sup>  | 7.1 ± 4.2 <sup>AD</sup>  | 20 ± 11 <sup>A</sup>      | 43 ± 27 <sup>D</sup>                |
| Water                   | Permanent lake or river  | –   | –  | –                         | –                                   |
| Road                    | Forest road  | –   | –  | –                         | –                                   |
| Others                  | All other weakly represented forest or non-forest polygons in the study area | –   | –  | –                         | –                                   |

<sup>a</sup> Following ecoforest maps.



direction. Vertical cover density was evaluated using cover proportion (10% classes) of canopy cover in a 50 cm × 50 cm quadrat held parallel to and at a distance of 2 m from the ground at 10 equidistant points each 3 m along the diagonal of the sampling plot (adapted from Vales and Bunnell, 1988). We estimated lateral cover density according to Nudds' (1977) method which consists in evaluating vegetation cover (10% classes) obstructing a 2-m high profile board. This measure was done at each cardinal point and at 15 m from the plot center.

For each variable considered to describe the retained habitat categories, we conducted an ANOVA (or ranked-ANOVA according to Conover's approach) followed by a Tukey multiple comparison test *a posteriori* in order to better identify differences between habitat categories. These analyses were done using SYSTAT 11.0 (SYSTAT Software Inc, 2004) statistical software.

### 3.3. Habitat selection

The study area was defined using the minimum convex polygon method (MCP 100%; Mohr, 1947) calculated for all locations from the 15 studied individuals. We used the same method to determine home range sizes. We preferred using the MCP method over the kernel method due to the important bias generated by the latter method during home range estimation based on a large number of locations, as usually obtained from GPS telemetry data acquisition (Hemson et al., 2005). These authors have shown that this bias is even more important when the studied individuals demonstrate fidelity to certain sectors of their home range. Moreover, the calculation of a 100% MCP was preferred instead of a 95% MCP due to the high accuracy of locations issued from GPS telemetry, and because locations showing a PDOP > 10 were deleted at first hand. For the eight individuals tracked during 2 complete years, we chose to estimate home ranges on a multiannual basis considering the overlap between annual home ranges for a same individual (i.e., >50% overlap) and we verified the absence of a significant effect of the year on habitat selection. Indeed, a preliminary multivariate analysis of variance (MANOVA) done on the eight individuals followed during a continuous 2-year period did not reveal any year effect at both spatial scales [i.e., at the study area scale ( $F = 3.25$ ;  $P = 0.08$ ) and at the home range scale ( $F = 0.84$ ;  $P = 0.59$ )]. Since an individual constitutes a sampling unit, this method allows us to control for temporal pseudoreplication in the habitat selection analyses. The MCPs were calculated using the Hawth's Analysis Tools extension in ArcGIS 9.0 (ESRI, 2004).

We studied habitat selection by forest-dwelling caribou at two spatial scales. At the scale of the study area [i.e., 2nd order of selection according to Johnson (1980)], the proportion of each habitat category within the home range was compared to the proportion of these categories within the limits of the study area. At the second spatial scale, which aims at detecting a selection within the home range [i.e., 3rd selection order according to Johnson (1980)], we compared the proportion of locations per habitat category to the proportion of these habitats within the home range. Habitat selection evaluation at the scale of the home range was verified according to predefined periods: calving (15 May to 14 June), summer (15 June to 14 September), rutting (15 September to 14 November), winter (15 November – 14 April) and spring (15 April – 15 May). To determine the calving period, we used the average date of calving from a neighboring population (Charlevoix, Québec, ~150 km south-west of the population under study) recorded between 2004 and 2006 (MRNF, unpublished data). Winter and spring periods were based on snow depth conditions and mean daily temperatures obtained from meteorological surveys conducted in the region between 2004 and 2006 (University of Québec at Chicoutimi, unpublished data). We carried

out the habitat selection analyses using Hotelling's  $T^2$  method (Aebischer et al., 1993), i.e., a MANOVA performed at each studied spatial scale without ratio calculation. When the MANOVA revealed a non-random habitat use, *t*-tests were done *a posteriori* in order to test the null hypothesis of an absence of significant difference between used and available proportions by habitat category. We considered individuals as sampling units (random factor) and used the period as a fixed factor during the home range selection analysis. All MANOVAs were done using SAS 9.1 (SAS Institute Inc, 2002) with a significance level of 0.05. We considered a tendency when  $P$  was <0.01.

## 4. Results

### 4.1. Habitat characterization

The tree basal area, stem density of the shrub layer, canopy closure and terrestrial lichen cover allowed the differentiation of the seven inventoried forest habitat categories (Table 1). First, 0–5 year-old clearcuts created a very open habitat type due to the low lignous stem density caused by recent logging. The 6–20 year-old clearcuts remained a fairly open habitat although a slightly greater number of regenerating stems characterized the habitat. Similarly, regenerating forest, being mainly dominated by balsam fir, was characterized by a basal area that showed a greater density of shrubby stems constituting an established regeneration. The 50–70 and 90–120 year-old forests constituted closed habitats for which the arborescent strata's basal area, dominated by black spruce, was significantly greater than in the other habitat categories. In these two mature forest types, the understory was much less dense than that observed in regenerating forest, but mean canopy closure was similar between regenerating and mature forests. Although similar to clearcuts in terms of basal area and canopy closure, peatlands constituted a natural open habitat having not experienced any anthropogenic disturbances and for which ground cover was representative of lowland humid habitat. Finally, open lichen woodlands constituted a mature and open habitat dominated by black spruce and were characterized by the highest proportion of ground lichen when compared to other categories (Table 1).

### 4.2. Habitat selection at the study area scale

The use of different habitat categories by forest caribou was non-random ( $F = 11.69$ ;  $P = 0.004$ ). When taking into account their availability at the scale of the study area, 90–120 year-old forests were overrepresented within the home ranges (use:  $26.1 \pm 1.2\%$  vs. availability: 21.7%), contrarily to 50–70 year-old forests that were underrepresented (use:  $16.0 \pm 1.6\%$  vs. availability: 20.4%) (Table 2). Also, a tendency for overrepresentation of 6–20 year-old clearcuts inside home ranges was observed ( $t = 1.92$ ;  $P = 0.076$ ).

**Table 2**

Mean use and availability ( $\pm$ S.E., %) of habitat categories by forest caribou ( $n = 15$ ) at the scale of the study area.

| Category                | Availability | Use            | <i>P</i> |
|-------------------------|--------------|----------------|----------|
| 0–5 year-old clearcuts  | 4.1          | $4.5 \pm 0.8$  | 0.640    |
| 6–20 year-old clearcuts | 18.9         | $23.9 \pm 2.6$ | 0.076    |
| Regenerating forests    | 5.8          | $1.8 \pm 0.4$  | <0.001   |
| 50–70 year-old forests  | 20.4         | $16.0 \pm 1.6$ | 0.016    |
| 90–120 year-old forests | 21.7         | $26.1 \pm 1.2$ | 0.002    |
| Peatlands               | 1.5          | $1.3 \pm 0.1$  | 0.070    |
| Open lichen woodlands   | 1.2          | $1.4 \pm 0.3$  | 0.391    |
| Water                   | 16.1         | $15.4 \pm 2.0$ | 0.735    |
| Road                    | 5.6          | $5.8 \pm 0.4$  | 0.568    |
| Others                  | 4.9          | $3.9 \pm 0.9$  | 0.290    |

**Table 3**Mean use and availability ( $\pm$ S.E., %) of habitat categories by forest caribou ( $n = 15$ ) at the home range scale.

| Category                | Availability   | Calving        |        | Summer         |        | Rutting        |        | Winter         |        | Spring         |        |
|-------------------------|----------------|----------------|--------|----------------|--------|----------------|--------|----------------|--------|----------------|--------|
|                         |                | Use            | P      | Use            | P      | Use            | P      | Use            | P      | Use            | P      |
| 0–5 year-old clearcuts  | 4.5 $\pm$ 0.8  | 4.7 $\pm$ 2.3  | 0.915  | 4.1 $\pm$ 2.0  | 0.852  | 5.5 $\pm$ 2.2  | 0.576  | 0.9 $\pm$ 0.4  | 0.002  | 4.1 $\pm$ 2.6  | 0.894  |
| 6–20 year-old clearcuts | 23.9 $\pm$ 2.6 | 16.1 $\pm$ 4.9 | 0.049  | 9.4 $\pm$ 4.0  | <0.001 | 14.7 $\pm$ 3.7 | 0.007  | 25.3 $\pm$ 3.4 | 0.582  | 39.7 $\pm$ 8.1 | 0.057  |
| Regenerating forests    | 1.8 $\pm$ 0.4  | 2.5 $\pm$ 1.8  | 0.732  | 1.3 $\pm$ 1.8  | 0.443  | 1.0 $\pm$ 0.6  | 0.206  | 0.4 $\pm$ 0.2  | 0.007  | 0.4 $\pm$ 0.4  | 0.037  |
| 50–70 year-old forests  | 16.0 $\pm$ 1.6 | 26.6 $\pm$ 6.5 | 0.074  | 27.8 $\pm$ 4.1 | 0.004  | 17.6 $\pm$ 3.6 | 0.588  | 12.9 $\pm$ 3.9 | 0.368  | 17.0 $\pm$ 6.8 | 0.866  |
| 90–120 year-old forests | 26.1 $\pm$ 1.2 | 31.2 $\pm$ 4.2 | 0.187  | 36.0 $\pm$ 4.5 | 0.028  | 34.6 $\pm$ 4.7 | 0.077  | 25.0 $\pm$ 2.6 | 0.603  | 19.1 $\pm$ 3.9 | 0.051  |
| Peatlands               | 1.3 $\pm$ 0.1  | 3.3 $\pm$ 0.9  | 0.030  | 3.2 $\pm$ 0.7  | 0.010  | 3.6 $\pm$ 0.7  | 0.002  | 1.7 $\pm$ 0.5  | 0.350  | 2.0 $\pm$ 0.9  | 0.396  |
| Open lichen woodlands   | 1.4 $\pm$ 0.3  | 4.7 $\pm$ 1.6  | 0.043  | 5.4 $\pm$ 1.8  | 0.032  | 14.0 $\pm$ 3.9 | 0.005  | 21.1 $\pm$ 4.5 | <0.001 | 4.0 $\pm$ 1.3  | 0.059  |
| Water                   | 15.4 $\pm$ 2.0 | 2.4 $\pm$ 0.8  | <0.001 | 4.3 $\pm$ 1.5  | <0.001 | 2.6 $\pm$ 0.6  | <0.001 | 7.3 $\pm$ 1.8  | 0.003  | 2.1 $\pm$ 0.9  | <0.001 |
| Road                    | 5.8 $\pm$ 0.4  | 5.1 $\pm$ 1.2  | 0.550  | 7.3 $\pm$ 2.7  | 0.574  | 3.7 $\pm$ 0.7  | 0.004  | 4.1 $\pm$ 0.5  | 0.004  | 6.0 $\pm$ 1.2  | 0.873  |
| Others                  | 3.9 $\pm$ 0.9  | 3.0 $\pm$ 1.5  | 0.597  | 0.8 $\pm$ 0.2  | 0.005  | 2.5 $\pm$ 1.3  | 0.354  | 0.9 $\pm$ 0.4  | <0.001 | 5.3 $\pm$ 3.8  | 0.647  |

#### 4.3. Habitat selection at the home range scale

Use of different habitat categories differed according to the studied periods ( $F = 5.89$ ;  $P < 0.001$ ). Caribou habitat use was comparable between calving, summer and rutting periods, between 15 May and 15 November (Table 3). During these three periods, open lichen woodlands and peatlands were selected. Inversely, 6–20 year-old clearcuts were always avoided (i.e., underutilized in proportion to their availability). Forest types 50–70 and 90–120 years old showed a tendency to be selected during the rutting period ( $t = 1.91$ ;  $P = 0.077$ ), while roads were avoided. Habitat use was different during winter compared to the three previous periods. Open lichen woodlands were selected ( $t = 4.63$ ;  $P < 0.001$ ) while 0–5 year-old clearcuts as well as regenerating forests and roads were avoided in winter. During spring, we found a tendency for caribou to select open lichen woodlands ( $t = 2.05$ ;  $P = 0.059$ ) and 6–20 year-old clearcuts ( $t = 2.07$ ;  $P = 0.057$ ), while a trend towards avoiding 90–120 year-old forests was observed as well ( $t = -2.13$ ;  $P = 0.051$ ). The regenerating forest was avoided during spring ( $t = -2.30$ ;  $P = 0.037$ ).

## 5. Discussion

In order to interpret efficiently our results in a management and conservation perspective, we must be aware of differences in caribou habitat use and habitat selection that previous studies highlighted across North America. Indeed, woodland caribou has shown different habitat use strategies in response to varying intensities of disturbance and loss of native forested habitats throughout its distribution range (e.g., Smith et al., 2000; Schaefer, 2003; Courtois et al., 2007). As examples, studies conducted in Alberta showed that woodland caribou home range size and daily movement rates both decreased following clear-cut logging (Smith et al., 2000), while in Québec, caribou travelled larger distances and expanded their home range to avoid fragmented landscapes (Courtois et al., 2007). However, although habitat use patterns differ regionally, similarities can be observed across North American woodland caribou populations inhabiting harvested landscapes: the avoidance of recently disturbed areas, probably to dampen predation risk (Chubbs et al., 1993; Vors et al., 2007).

Woodland caribou is generally associated to mature coniferous forests (Chubbs et al., 1993; Apps et al., 2001; Ferguson and Elkie, 2004; Wittmer et al., 2007) and to fen/bog complexes (Stuart-Smith et al., 1997; James et al., 2004; McLoughlin et al., 2005), but patterns of habitat selection vary from western to eastern North America according to differences in management strategies and forest structure and composition across boreal forest (Smith et al., 2000; Schaefer, 2003; Courtois et al., 2007). Indeed, in western Canada, the distribution of the mountain caribou ecotype appeared to be related to the distribution of >140 years-old cedar/hemlock

and spruce/subalpine fir forests (Apps and McLellan, 2006) while Rettie and Messier (2000) have observed a strong preference toward peatlands and black spruce forests in Saskatchewan. Similar conclusions were obtained in Newfoundland where woodland caribou select mature forests (mainly balsam fir stands of >80 years-old), while avoiding recent clearcuts (0–20 years-old) and early successional stages (20–40 years-old balsam fir stands) (Mahoney and Virgl, 2003). However, although several studies have described habitat use and habitat selection of woodland caribou (migratory and mountain ecotypes), few have characterized habitat use and habitat selection for forest-dwelling caribou (sedentary woodland caribou) in highly managed landscapes.

#### 5.1. Habitat selection at the study area scale

In accordance with our general hypothesis, 90–120 year-old forests constituted the habitat type sought after by caribou at the scale of the study area. Many studies have already shown this selection behavior for mature forests (e.g., Rettie and Messier, 2001; Mahoney and Virgl, 2003; Ferguson and Elkie, 2004), explaining it by the adoption of an anti-predator strategy. Indeed, in the absence of migratory behavior, sedentary caribou diminish predation risk by using habitats that allow them to spatially isolate themselves from alternative prey, and consequently from predators (Rettie and Messier, 2000). Wittmer et al. (2007) have demonstrated that the mortality rate associated with predation was lower in females for which the home range showed an important proportion of mature forest. Based on these studies, the selection of 90–120 year-old forests by caribou could be to limit the spatial overlap with alternative preys, such as moose, in order to lower predation risk. Although representing the least fragmented closed forest habitat in the study area (see Fig. 1B), 50–70 year-old forests were not selected by caribou. The highly heterogeneous distribution of 50–70 year-old forests could partly explain this result. This forest category is not usually considered in caribou habitat selection studies. Nevertheless, by dissociating it from older mature forests, we have been able to exclude its confounding effect and absence of selection.

The underrepresentation of regenerating forests (20–40 years old) within home ranges also supports the hypothesis of an anti-predation strategy. In the black spruce – moss domain, regenerating areas issued from forest clearcuts or natural disturbances (e.g., fires, insect epidemics and windfalls) are often colonized by deciduous species associated with black spruce such as white birch and trembling aspen (Gagnon and Morin, 2001). Because of their vegetation composition, regenerating forests can be a favorable food source for moose (Courtois et al., 1998). Caribou seemed to favor the establishment of their home range in sectors where the proportion of regenerating forests was inferior to their availability, therefore potentially limiting encounters with predators.

Certain studies conducted in disturbed landscapes have shown that caribou avoid establishing their home range in sectors where logging is common (e.g., Chubbs et al., 1993; Smith et al., 2000; Courtois et al., 2003). Indeed, logged areas should, in general, be avoided by caribou because of the presence of early successional vegetation types favorable to moose and black bear. In contradiction to these studies and to our general hypothesis, our results show the tendency of 6–20 year-old clearcuts to be overrepresented in home range selection at the study area level. Following similar results in the province of Saskatchewan (Canada), Rettie and Messier (2000) proposed that habitat selection could be further explained by the distribution of individuals before disturbance than by a preference for available habitats after disturbance. Although the existence of a philopatric behavior in forest caribou has not yet been demonstrated in the Québec boreal forest, the selection of logged areas in the short or long term could reflect a fidelity by caribou to their annual and seasonal home ranges that were established before disturbance, such as observed in many other Canadian provinces (Schaefer et al., 2000; Rettie and Messier, 2001; Wittmer et al., 2006).

Nevertheless, while observing the mapping of habitat categories under study, the overrepresentation of 6–20 year-old clearcuts in the home ranges could be further attributed to their importance and distribution in the landscape. In support of this hypothesis, a landscape analysis done *a posteriori* has revealed a strong spatial association between 6–20 year-old clearcuts and 90–120 year-old forests in the study area (see details in Appendix A). This association seems attributable to the logging strategy and residual forest distribution that has been used in Québec for the past 20 years (Fig. 1B). Indeed, following current forest regulations, residual forest adjacent to clearcuts (varying in size from 50 to 150 ha) were mainly conserved in the form of 60–100 m wide linear strips (Gouvernement du Québec, 2003). Combined to the uniform distribution of logged areas, the spatial association of 6–20 year-old clearcuts with mature residual forest can complicate the avoidance of this former type of habitat by caribou (Fig. 1B). Indeed, an analysis of distances done *a posteriori* showed that caribou locations in clearcuts were not distributed in a random manner; these being more frequently located near residual forest borders [ $141.7 \pm 5.2$  m (S.E.)] comparatively to random points [ $181.5 \pm 7.0$  m (S.E.)] (Mann–Whitney  $U = 2.17 \times 10^8$ ;  $P = 0.001$ ). This caribou distribution pattern suggests that in forest landscapes greatly impacted by harvesting activities, the inclusion of logged areas in the home range of caribou becomes inevitable during the location process for 90–120 year-old forests. In the long term, Vors et al. (2007) reported a 20 year interval between the completion of a clearcut and the permanent abandonment of a harvested boreal forest landscape by caribou. Based on this result, we observed that clearcutting inside the study area began in 1985 (therefore <20 years before the onset of the study), suggesting that the negative cumulative effect of anthropogenic disturbances on the distribution of caribou at the scale of the study area and of the landscape can accentuate with time.

## 5.2. Habitat selection at the home range scale

Habitat selection at home range scale varied between periods, probably reflecting different needs of caribou during different periods of its vital cycle (Courtois, 2003). During calving, caribou selected open lichen woodlands and peatlands while avoiding 6–20 year-old clearcuts. These results agree with those of other studies suggesting that predator avoidance is the main driving force of female caribou habitat selection during the calf vulnerability period early after birth (e.g., Barten et al., 2001; Lantin, 2003). Indeed, use of naturally open areas, such as open lichen woodlands and peatlands, has already been associated to a strategy which limits encounter probabilities with predators and alternative prey (Stuart-Smith

et al., 1997; McLoughlin et al., 2005). In contrast, disturbed areas can increase predation risk since mature forest cover lost to the benefit of early successional vegetation is favorable to alternative preys (Rettie and Messier, 1998). Moreover, Courtois et al. (2007) have demonstrated an increase in movement and seasonal home range size in a disturbed landscape, mainly during calving. This dispersal behavior may reflect caribou's need to isolate themselves from predators in order to increase calf survival (Barten et al., 2001; Ferguson and Elkje, 2004). Our results thus support the hypothesis that predator avoidance constitutes the main factor driving habitat selection during calving.

Selection patterns were similar during calving and summer. Caribou selected open lichen woodlands and peatlands and avoided 6–20 year-old clearcuts, possibly limiting predation pressure on newborn calves. In contrast, caribou selected closed-canopy forests (50–70 and 90–120 year-old forests) more often during summer. Besides, mature conifer forests are known to be a major component of caribou summer habitat (Servheen and Lyon, 1989; Chubbs et al., 1993). On one hand, mature coniferous forests are less favorable to alternative preys and consequently, such selection behavior possibly leads to a lower predation pressure on calves (e.g. Rettie and Messier, 1998; James et al., 2004). In addition, Seip (1992) has demonstrated that wolf predation pressure on mountain caribou of British-Columbia became very important during summer. On the other hand, these areas have abundant food resources that are revealed by the diversity of the summer diet of caribou (Rettie and Messier, 2000; Lantin, 2003), mainly composed of grasses, terrestrial lichens and deciduous and ericaceous plants (Russell et al., 1993). The works of Lantin (2003), done on the Québec-Ontario province limits, suggested that habitat variables describing available forage were more important in calf survival than variables associated to protection cover. Following these studies, the best strategy for forest-dwelling caribou would be to use mature coniferous forests and naturally open areas during summer as these habitats possibly represent the best tradeoff between predator avoidance and foraging activities.

During the rutting period, open lichen woodlands and peatlands were the habitat types mainly frequented by caribou. These habitats consist of vast, generally open, lands that facilitate the search for partners (Courtois, 2003). In winter, however, female concentration in open lichen woodlands could be further explained by foraging behavior, these xeric areas sustaining an important biomass of terrestrial and arboreal lichens (Table 1; Sulyma and Coxson, 2001). Johnson et al. (2001) as well as Lantin (2003) have also demonstrated that sites rich in terrestrial lichens are favored by caribou during winter. In an adjacent population (Charlevoix, Québec), winter frequentation of open areas rich with terrestrial lichens normally lasts until snow depth conditions do not allow the digging of feeding craters (Vandal, 1985). On another note, the use of 6–20 year-old clearcuts during spring suggests a change in diet. Indeed, these recently clearcut areas are flushed with vegetation regrowth (e.g., grasses and deciduous plants) that are favored by caribou especially after a long period of a diet consisting mainly of lichens (Servheen and Lyon, 1989).

## 5.3. Synthesis

In agreement with our general hypothesis, our results suggest that coniferous mature forests are an essential element in the habitat selection process by forest caribou at both scales. Although closed mature forests of 90–120 years are strongly selected at a large scale, such a selection seems less marked at the home range scale to the benefit of a more open mature forest: the open lichen woodlands. Considering that open lichen woodlands correspond to mature spruce stands showing a tree density <25% and a lichen



ground cover >40%, it appears that these areas are located within the mature forest mosaic. This underlines the importance of conserving large patches of forest >90 years old in the areas frequented by caribou. In counter part, the overrepresentation of clearcut areas in the home ranges of caribou did not match our hypothesis, these habitat categories being difficult to avoid at the scale of the study area. Our results clearly show that 6–20 year-old clearcuts were not avoided at the large scale of selection probably because they were associated with mature forests, suggesting a landscape configuration effect on habitat selection. At the home range scale, we showed how much habitat choices made by caribou varied in time, on an interannual basis, possibly reflecting the specific needs linked to their life cycle.

## 6. Management implications

For a variety of species, many authors have shown that the maintenance of viable populations in a disturbed landscape does not uniquely depend on the conservation of a minimal amount of various habitat types, but that the spatial organization of the habitat types within the managed forest mosaic could be greatly determining in regard to the distribution of populations (Rempel et al., 1997; Lindenmayer and Franklin, 2002; O'Brien et al., 2006). Our results suggest such an effect of the spatial configuration of mature forest and clearcuts on habitat selection by forest-dwelling caribou. Present forest exploitation rates force caribou to frequent clearcut areas in order to reach 90–120 year-old forests, which are only presently available as residual mature forest strips of less than 60 m width. In constraining caribou to use lower quality habitats where predation risk could be greater, the current forest harvesting strategy might correspond to an ecological trap (Battin, 2004) that could accelerate the northern range recession of forest-dwelling caribou. Although the impacts of the spatial association between clearcuts and 90–120 year-old forests on the maintenance of the studied caribou population can be difficult to determine, our results underline the relevance of developing a new strategy for distributing clearcuts within the landscape. Ideally, this strategy would aim for the grouping of cuts at the landscape scale in order to allow for the conservation of large unfragmented old forest stands (e.g., whole block units >250 km<sup>2</sup>; Courtois, 2003). Such a strategy is actually under study in Québec and could reduce the northern range recession of forest-dwelling caribou.

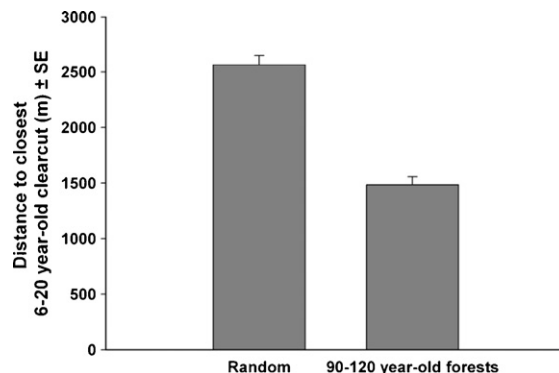
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## Appendix A

Description of the landscape analysis aimed at verifying spatial association between 90–120 year-old forests and 6–20 year-old clearcuts by comparing the mean minimal distance between 6–20

year-old clearcuts and 90–120 year-old forests, and between 6–20 year-old clearcuts and a series of random points. Using ArcGIS 9.0 (ESRI, 2004), the minimal distance between each 90–120 year-old forest polygon centroid and 6–20 year-old clearcut polygon borders was determined to allow for the calculation of a mean minimal distance. This same step was done between 1000 random points and the 6–20 year-old clearcut polygon borders. The two mean minimal distances generated were compared using a Mann–Whitney (Zar, 1999) non-parametric test. It appears that the mean minimal distance between the 90–120 year-old forests and 6–20 year-old clearcuts was significantly smaller than the one calculated between random points and 6–20 year-old clearcuts ( $U = 655,477$ ;  $P < 0.001$ ). Our results suggest a non-random distribution of the 90–120 year-old forests in relation to the 6–20 year-old clearcuts.



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